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Pseudoscolia: A Spheciform Wasp with a Pointed Glossa (Hymenoptera: Crabronidae)

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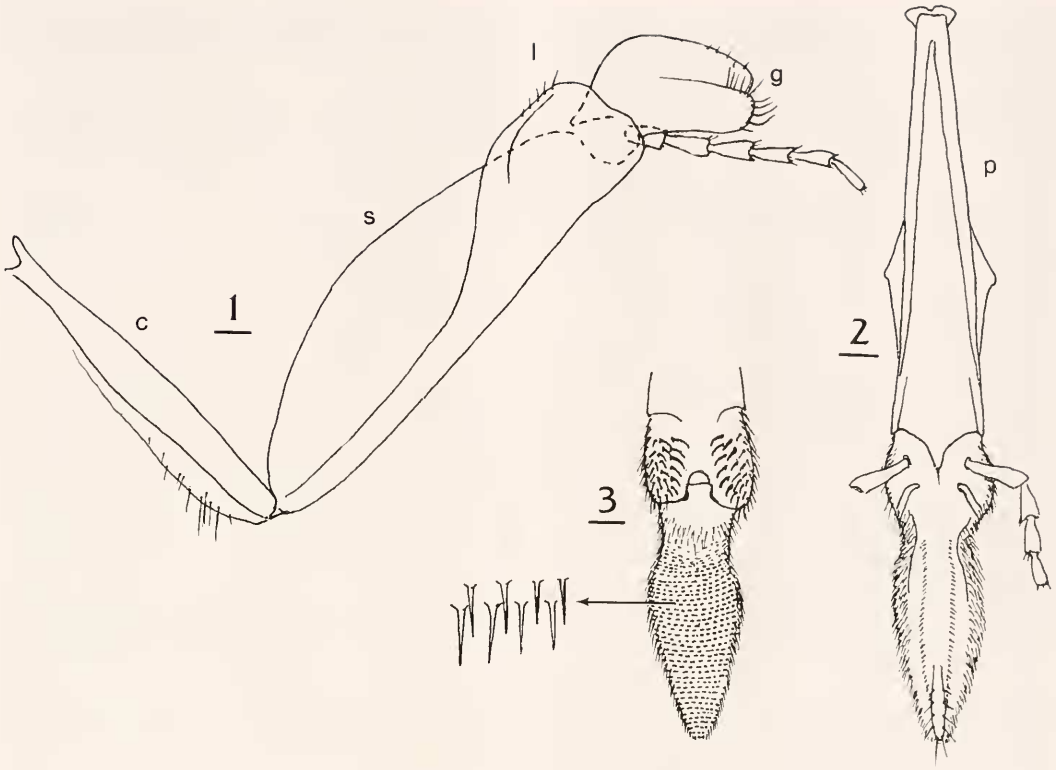
Abstract.—The philanthine genus *Pseudoscolia* Radoszkowski differs from other apoid wasps in having a narrow, pointed glossa similar in details to that of many short-tongued bees. Its other characters, however, even those of other mouthparts, resemble those of other philanthine wasps. Therefore the glossal shape of *Pseudoscolia* is presumably not homologous to that of bees, but was independently derived from the truncate or bilobed wasp glossal shape. Such a shape in colletid bees is not homologous to that of wasps, but is believed to be based on a different part of the glossa. The pointed glossa of *Pseudoscolia* suggests that it is reasonable to speculate that the ancestral bee had a pointed glossa.

On reading a paper by Prentice and Pulawski (2004), I was surprised to learn that there exists a genus (*Pseudoscolia* Radoszkowski) of philanthine wasps with a pointed glossa, a fact curiously ignored in major works on the group (Bohart and Menke 1976; Alexander 1992). Although named in 1876 and with 35 currently recognized species (W. Pulawski, pers. comm.), *Pseudoscolia* was first recognized as having a pointed glossa by Prentice (1998) in an as yet unpublished resource. Other spheciform wasps (i.e., wasps in the superfamily Apoidea, or apoid wasps) have the broad truncate or bilobed glossal shape characteristic of most Hymenoptera. The existence of a spheciform wasp with a pointed glossa is of interest to students of bee evolution because there are two views about the glossal morphology of the ancestral bee, i.e., the protobee from which modern bees evolved. One view is that it had a truncate or bilobed glossa like that of spheciform wasps (other than *Pseudoscolia*), and as do all females and nearly all males of the modern bee family Colletidae. The spheciform wasps are the paraphyletic group from within which the bees arose (for more information see below). The truncate or bilobed glossa is the principal character indicating that the Colletidae, having retained as a plesiomorphy the broad glossa from wasp ancestors, is the basal branch of the bee phylogeny, the sister group to all other bees. The alternative view is that the ancestral bee had a pointed glossa and that the truncate or bilobed glossa of Colletidae is a derived feature used by females for painting the cell lining onto the walls of the brood cells (something wasps do not do). Such a broad glossa is similar in shape to that of the wasps, but under this scenario would be interpreted as a synapomorphy rather than a plesiomorphy of the Colletidae.

Although not obvious in all colletids, it appears that the preapical fringe of the colletid glossa is at the apex of the annulate or anterior surface of the glossa and that the more distal, commonly bilobed part of the glossa and the glossal brush are derived from the disannulate posterior surface (terminology of Michener and Brooks 1984). In apoid wasps, however, the annulate anterior surface extends to the distal margin; there is no preapical



Figs 1–3. 1. Inner view of maxilla of *Pseudoscolia dewitzii*. The galea, which is actually turned obliquely, is turned to same plane as the stipes for illustration. c, cardo; s, stipes; l, lacinia?; g, galea. 2. Posterior view of labium. The mentum is directed away from the observer from the base of the prementum. p, prementum. 3. Anterior view of glossa and paraglossal area. Only the conspicuous bases of the annular hairs are shown; the transparent and almost invisible annular hairs are enlarged at the left.

fringe and no glossal brush, although apical setae may resemble a sparse brush. Thus it appears on anatomical grounds that the broad, usually bilobed apex of the glossa is different in derivation in wasps and in colletid bees. Unfortunately there are colletids in which the anatomical evidence is not very clear (see Michener 1992), so the above interpretation, while probable, is not unassailable.

Recent works have provided a basis for understanding the phylogeny of major lineages of aculeate Hymenoptera. The superfamily Apoidea (apoid or spheciform wasps and the bees) is monophyletic, as shown by Melo (1999) and Brothers (1975). The Apoidea is divisible into the following families: Heterogynaidae, Ampulicidae, Sphecidae *s. str.*, Crabronidae, Colletidae, Stenotritidae, *Andrenidae, *Halictidae, *Melittidae, *Megachilidae, and *Apidae (Michener 2000a: 60). The first two are groups with plesiomorphic characters such that they are basal branches of cladograms for apoid families. The Sphecidae *s. str.* forms the next branch, the sister group to the remaining families, Crabronidae + the bees. [Lomholdt (1982), who recognized the relationships among the bees and the paraphyletic group called spheciform wasps, used the name Larridae for the group now called Crabronidae.] Finally the Crabronidae is the sister group to the bees. Some authors such as Lomholdt (1982), Gauld and Bolton (1988), and Melo (1999) prefer to unite bees under

the family name Apidae *s. lato.* Synapomorphies for the bees as a whole, separating them from the Crabronidae, are listed by authors such as Melo (1999), Roig-Alsina and Michener (1993), Alexander and Michener (1995), and Michener (2000a, b). As to apomorphies of Crabronidae, the most striking is the bifid salivary opening of the larva, differing from that of bee larvae as well as other Hymenoptera.

Of the families of the superfamily Apoidea listed above, those marked by asterisks have pointed glossae, certainly a derived feature relative to the broad glossa of other Hymenoptera. As indicated above, recent authors (Radchenko and Pesenko 1994, 1996; Michener 2000a, b) doubt the view that the shape of the broad colletid glossa is homologous to the similar shape of the glossa of wasps. This doubt was first developed because three genera of obvious colletid bees have pointed glossae in males, suggesting that the broad glossa of Colletidae arose first in females in connection with application of the cellophane-like brood cell linings characteristic of nests of Colletidae. Perkins (1912) and McGinley (1980) were the first to suggest that the pointed glossa of a few male colletids might be ancestral for bees, hence the appellation "Perkins-McGinley Hypothesis."

MATERIALS AND METHODS

A male and a female of *Pseudoscolia dewitzii* (Kohl) from Egypt, determined by W. J. Pulawski, were used. The mouthparts and terminalia were dissected out, treated mildly with KOH solution at room temperature, washed in water, and studied in glycerin, using magnifications up to 200×. For comparison, specimens of *Cerceris compacta* Cresson, *Philanthus bicinctus* Mickel and *P. gibbosus* (Fabricius) were similarly treated.

The proboscis is regarded as projecting downward from the head. Thus the anterior surface of the glossa is the surface that would be dorsal if the proboscis were considered to project forward, and the posterior surface would be called ventral in that case.

The terminology used for glossal structures is that of Michener and Brooks (1984). I use the word 'seta' for a hair-like projection arising from a socket-like base, and the word 'hair' for such a projection not arising from a socket, its base spreading onto the cuticular surface.

GENUS *PSEUDOSCOLIA*

This genus of philanthine wasps is found from the Canary Islands and North Africa east through the Middle East and Central Asia to eastern Siberia, and south to Kenya (Prentice and Pulawski 2004). It is a basal member of the *Cerceris* clade, the tribe Cercerini, according to Alexander (1992). Except for the glossa, its characters are those of related Crabronidae and not those of bees. Thus the setae are simple, the hind basitarsus is slender, the seventh metasomal tergum of the female is continuous dorsally (not divided into lateral hemitergites as in bees), the posterior strigil of the hind leg is present (although weakly developed), the seventh and eighth metasomal sterna of the male are not modified as in bees, bristles are numerous on the outer surfaces of the middle and hind tibiae, and the pretarsal claws are simple (not cleft as in many bees). Wasp systematists tend to give little attention to the labiomaxillary complex which in dead specimens is often retracted and hard to study. However, it is reasonable to believe that all species of the genus have an acute glossa; Prentice and Pulawski (2004) mention the acute glossa as a generic character. W. J. Pulawski kindly checked all 23 species of *Pseudoscolia* in the collection of the California Academy of Sciences; in two species the glossa was hidden but in 21 the glossa was pointed (pers. comm.).

In *Pseudoscolia dewitzii* the maxilla (Fig. 1) is much like that of related wasps. The galea is short, not elongate in company

with the glossa, as is common in bees. The galeal comb is reduced to a few bristles; probably homologous to the better developed comb of *Philanthus*, *Cerceris* and most Crabronidae, but not homologous to the more basal galeal comb of many short-tongued bees. It is possible that the small size of *P. dewitzii* is associated with the reduction of some structures (such as galeal comb and paraglossa) relative to those of *Philanthus* and *Cerceris*.

Because of the short galeae, the glossa protrudes by itself (Figs. 1, 2). One wonders how it functions; in short-tongued bees with a pointed glossa the galeae generally form a partial sheath around the glossa, movements of which apparently draw up the nectar (Harder 1983). The labium, including the glossa, are shown in Figure 2; the mentum is directed at right angles away from the observer at the base of the prementum and is therefore scarcely shown. [Galeae are also elongate in the Sphecidae s. str. such as *Ammophila* which have a long but bifid glossa (Ulrich 1924).]

The distal parts of the paraglossae are greatly reduced compared to *Philanthus* and *Cerceris* but their basal parts are broad and armed with coarse, blunt, curved, spine-like setae (Fig. 3) on the anterior surfaces.

The glossa is remarkably similar to that of short-tongued non-colletid bees (i.e. families Andrenidae, Halictidae, Melittidae). The anterior surface of the glossa is transversely annulate (Fig. 3), the annuli evident because of the transverse rows of bases of the annular hairs. The annular hairs are simple, tapering to sharp points. Laterally the annuli extend around the sides of the glossa and end in abundant marginal hairs, much as in Fig. 5 of Michener and Brooks (1984).

The disannular surface of the glossa is a delicate membrane that occupies much of the posterior surface (Fig. 2). It lacks annuli and annular hairs (except perhaps laterally where it is difficult to judge whether annuli extend onto the posterior surface among dense marginal hairs). Mesal to the marginal hairs the posterior surface the glossa is hairless except for two rows of seriate hairs (Fig. 2) which are short, simple and divergent, being directed distolaterally. The seriate hairs mark the seriate lines of Michener and Brooks (1984).

An elongate, weakly sclerotized body, probably to be called a flabellum, lies on the apex of the posterior surface of the glossa; it bears pairs of setae laterally (Fig. 2). A remarkably similar flabellum is found in *Ctenoplectra* (Fig. 57, Michener and Brooks 1984) but in that melittid bee it extends distally beyond the apex of the rest of the glossa, as does a typical flabellum. The distinctive sensilla of the basiglossal sclerite of bees are not evident in *Pseudoscolia*. In contrast to many colletid bees (Michener 1992), there are no obvious sexual differences in the glossa of *Pseudoscolia*.

DISCUSSION

The elongate, pointed glossa of *Pseudoscolia* is presumably an apomorphy of the genus and its shape is almost certainly not homologous to the shape of the pointed glossa in the bee families Melittidae, Andrenidae, Halictidae, the long-tongued bees, and also in a few male Colletidae. Its importance for understanding bee phylogeny is that it demonstrates that it is not outlandish to believe that the protobee (a close relative of, perhaps sister to, the Crabronidae) had a pointed glossa. Such a glossa is not in the ground plan of the Crabronidae, but since it evolved within that family (producing *Pseudoscolia*), there might have been the potential for the evolution of a very similar complex structure in the sister group, ancestors of modern bees. The pointed glossa could then have been retained in most bees but was replaced by an independently evolved broad, truncate or bilobed glossa in female Colletidae and in males also except for three genera of Hylaeinae.

It is probable that the Hylaeinae is not

a basal subfamily of Colletidae (Alexander and Michener 1995) although its lack of a scopa and transfer of pollen in the crop have sometimes been interpreted as ancestral. If the Perkins–McGinley hypothesis is supported, one must assume that the broad colletid glossa arose as a female character in ancestral Colletidae and that it was transferred at various times to nearly all male colletids, for which it has no known special function. In other words, loss of the pointed glossa in males occurred more than once in colletid evolution, since maintenance of separate glossal structures for the two sexes was not advantageous.

It has to be admitted that the independent origin of a pointed glossa in *Pseudoscolia* could be interpreted to mean that the pointed glossae of males of three hylaeine colletid genera could also have arisen independently from the similar pointed glossae of most families of bees. There is no reason to believe, however, that a pointed glossa would be advantageous for male colletids; it seems more like a relic than a novelty.

In contrast to the wasps, whose broad glossa is annulate to the apex on the anterior surface and bears some long apical setae, that of colletids seems to end with extension of the posterior disannulate surface and the glossal brush. The detail of structure in which the pointed glossa of *Pseudoscolia* resembles that of the bee families Andrenidae, Halictidae and Melittidae is remarkable. It is not surprising that when the broad glossa was narrowed for whatever reason, whether for most bees or for *Pseudoscolia*, the ends of the annuli curved onto the sides and the setae scattered across the apex of the broad glossa were concentrated on the midapical flabellum. But how does it happen that the seriate lines and hairs, with no obvious homologues in the broad glossa of other Crabronidae, are as distinct in *Pseudoscolia* as in short-tongued bees?

It would be interesting to observe the functioning of the glossa of *Pseudoscolia*, for example to see if these wasps obtain nectar from different flowers or in different ways than do other Crabronidae of similar size.

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